Magneto-Aerotaxis in Marine Coccoid Bacteria

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ABSTRACT Magnetotactic cocci swim persistently along local magnetic field lines in a preferred direction that corresponds to downward migration along geomagnetic field lines. Recently, high cell concentrations of magnetotactic cocci have been found in the water columns of chemically stratified, marine and brackish habitats, and not always in the sediments, as would be expected for persistent, downward-migrating bacteria. Here we report that cells of a pure culture of a marine magneto-tactic coccus, designated strain MC-1, formed microaerophilic bands in capillary tubes and used aerotaxis to migrate to a preferred oxygen concentration in an oxygen gradient. Cells were able to swim in either direction along the local magnetic field and used magnetotaxis in conjunction with aerotaxis, i.e., magnetically assisted aerotaxis, or magneto-aerotaxis, to more efficiently migrate to and maintain position at their preferred oxygen concentration. Cells of strain MC-1 had a novel, aerotactic sensory mechanism that appeared to function as a two-way switch, rather than the temporal sensory mechanism used by other bacteria, including *Magnetospirillum magnetotacticum*, in aerotaxis. The cells also exhibited a response to short-wavelength light ($\leq$500 nm), which caused them to swim persistently parallel to the magnetic field during illumination.

INTRODUCTION

Magnetotactic bacteria contain magnetosomes, magnetic iron oxide or iron sulfide crystals enclosed in a membrane, that cause them to orient and migrate along geomagnetic field lines (Blakemore et al., 1989). In some magnetotactic spirilla, such as *Magnetospirillum magnetotacticum*, cells are oriented by the local magnetic field (**B**), and swim parallel or antiparallel to **B** in aerotactic bands (Spormann and Wolfe, 1984). In a homogeneous medium, roughly equal numbers of cells swim in either direction along **B** (Spormann and Wolfe, 1984; Blakemore et al., 1979). In contrast, freshwater and marine, bilophotrichously flagellated (having two flagellar bundles on one hemisphere of the cell), magnetotactic cocci swim persistently in a preferred direction relative to **B** (Blakemore, 1975; Moench and Konetzka, 1978; Kalmijn and Blakemore, 1978; Frankel, 1984). This persistent swimming led to the discovery of magnetotaxis in bacteria (Blakemore, 1975), and is the basis for the standard assay for magnetotaxis, i.e., microscopic examination of the response of swimming bacteria in water drops to changes in the direction of **B** (Blakemore and Frankel, 1981). Magnetotactic cocci in the Northern hemisphere swim parallel to **B** (north-seeking motility), whereas magnetotactic cocci in the Southern hemisphere swim antiparallel to **B** (south-seeking motility), which would cause them to migrate downward along the downward- and upward-inclined geomagnetic field lines in the respective hemispheres (Blakemore et al., 1980). Thus the function of magnetotaxis in magnetotactic cocci has

been thought to be facilitation of downward-directed migration for these bacteria in the water column, toward the microaerobic or anaerobic sediments, and away from higher oxygen concentrations ([O_2]) at the water surface (Blakemore, 1975; Blakemore et al., 1980; Blakemore and Frankel, 1981). However, large numbers of north-seeking cocci have recently been found in the water columns of chemically stratified, marine and brackish, semianaerobic basins at specific depths corresponding to the oxic-anoxic transition zone (OATZ) (Stoltz, 1992; Bazylinski et al., 1995). This raises the question of how these bacteria maintain their position at the OATZ in the water column, instead of migrating persistently down along the geomagnetic field to the bottom sediments (Frankel and Bazylinski, 1994).

We report here that cells of a bilophotrichously flagellated, magnetotactic marine coccus, designated strain MC-1, isolated from the OATZ of a semianaerobic basin and grown in pure culture, can swim in both directions along **B** without turning around. Like cells of *M. magnetotacticum*, MC-1 cells form microaerophilic, aerotactic bands (Meldrum et al., 1993). Most microaerophilic bacteria form aerotactic bands at a preferred or optimal [O_2], where the proton motive force is maximum (Zhulin et al., 1996), using a temporal sensory mechanism (Segall et al., 1986) that samples the environment as they swim and compares the present [O_2] with the [O_2] in the recent past (Taylor, 1983). The change in [O_2] with time determines the sense of flagellar rotation (Manson, 1992). Although the aerotactic behavior of *M. magnetotacticum* is consistent with the temporal sensory mechanism, the aerotactic behavior of cells of strain MC-1 is not. Instead, their behavior fits a novel model for a two-state aerotactic sensory system in which the [O_2] determines the sense of flagellar rotation and hence the swimming direction relative to **B**. This model, polar magneto-aerotaxis, accounts for the ability of cells of strain

MC-1 to migrate to, and maintain position at, the preferred $[O_2]$ at the OATZ in chemically stratified, semianaerobic basins.

MATERIALS AND METHODS

Strain MC-1, a Gram-negative magnetotactic coccus (DeLong et al., 1993), was isolated from the OATZ in the Pettasquamscutt estuary in Narragansett Bay, Rhode Island (Donaghay et al., 1992). Cells were grown in a semi-solid medium containing 5 ml of modified Wolfe's mineral solution (Wolin et al., 1963), modified by increasing $Na_2MoO_4 \cdot 2H_2O$, from 0.01 g to 0.4 g L^{-1}, and $CuSO_4 \cdot 5H_2O$ from 0.01 g to 0.02 g L^{-1}, and by the addition of 0.01 g L^{-1} $NiCl_2 \cdot 6H_2O$; 0.5 ml of a vitamin solution containing 90 mg thiamine, 40 mg inositol, 4 mg D,L-calcium pantothenate, 5 mg p-aminobenzoic acid, 5 mg vitamin B_{12}, 4 mg pyridoxine, 4 mg niacin, 0.1 mg biotin, and 0.04 mg folic acid in 100 ml of distilled, deionized water; 2.0 ml of 0.01 M ferric quinate (3); 0.25 g NH_4Cl; 2.5 g $Na_2S_2O_3 \cdot 5H_2O$ (the presumed energy source); 1.5 ml of 0.5 M potassium phosphate buffer, pH 7.0; 0.2 g $NaHCO_3$ (the sole carbon source); and 2 g of agar per liter of an artificial seawater mixture (Bazylinski et al., 1993). The pH of the growth medium was adjusted to ~7.1. Cells were injected by syringe into test tubes that were about two-thirds filled with this medium. The headspace was air and the tube caps were screwed on tightly. Consumption of oxygen by the cells generated an $[O_2]$ gradient in the culture tubes, and the cells grew as a microaerophilic band below the agar surface (Fig. 1 A). When resazurin was added to the medium (2 mg/L of growth medium), the band of cells was found to occur below the meniscus at the interface of the oxidized (pink) and reduced (colorless) forms of resazurin, indicating that the band formed at the OATZ in the tubes. If the band was disrupted by swirling or stirring with a sterile needle, it reformed in ~10 min, but took twice as long if the local magnetic field was reduced with a mu-metal shield. Bacteria were subsequently removed from the band with a sterile syringe and examined by light and transmission electron microscopy (TEM).

For TEM, cells were placed onto Formvar-coated, copper electron microscopy grids and allowed to settle for ~10 min. Excess liquid was removed with a piece of filter paper, and before each grid was completely dry, a drop of negative stain (a 2% ammonium molybdate solution containing 1% trehalose (Harris et al., 1996) at pH 7.0) was applied for ~5 s and blotted off. The grids were allowed to dry and were examined with a JEOL model 1200EX scanning transmission electron microscope operating at 100 keV.

Magnetospirillum magnetotacticum (ATCC 31632) was purchased from the American Type Culture Collection. Cells of this strain were grown microaerobically under 1% O_2 in minimal salts growth medium (American Type Culture Collection, 1989) containing the modified Wolfe's mineral solution described above.

North-seeking cells of strain MC-1 were magnetically selected by suspending cells in drops of the sterile growth medium, described above, containing 0.025% agar, and directing them to one edge of the drop with stirring bar magnets. These cells were drawn up into optically flat, glass capillary tubes with rectangular cross section (0.2 mm × 5 mm; VitroCom, Mountain Lakes, NJ). One end of the filled capillary tube was sealed with petroleum jelly, the other end was left open, resulting in an $[O_2]$ gradient along the tube (Fig. 2, top).

Cells of *M. magnetotacticum* were harvested by centifugation at 10,000 × g at 4°C and resuspended in ice-cold, fresh sterile minimal salts growth medium or 50 mM potassium phosphate buffer, pH 7.0, to a cell density of ~5–6 × 10^9 cells ml^{-1}. These cells were drawn up into the flat glass capillary tubes, which were treated as described above for cells of strain MC-1.

The filled capillary tubes were examined at low magnification with a dissecting microscope, and at higher magnification with a phase-contrast microscope, both fitted with a video camera and video cassette recorder. The dissecting microscope was fitted with two wire coils in the Helmholtz configuration, which produced a magnetic field of several gauss in the focal plane of the microscope; the direction of **B** was determined by the

direction of current in the coils. Dark-field illumination was provided by an external light source with a red-light filter (λ_{min} = 600 nm). The capillary was housed in a glass perfusion cell connected to a source of nitrogen gas or air, to control the $[O_2]$ in the capillary (Fenchel, 1994; Zhulin et al., 1996).

RESULTS

Using light microscopy and the standard assay in hanging drops to determine magnetotaxis, cells of strain MC-1 removed from growth cultures containing microaerophilic bands of cells were predominantly north-seeking (>1000:1, north-seeking cells to south-seeking cells), that is, they migrated persistently parallel to **B** and accumulated at the edge of the drop.

Cells of MC-1 contained a single chain of magnetite (Fe_3O_4)-containing magnetosomes (Meldrum et al., 1993) (Fig. 1 B), typically oriented perpendicular to a line drawn between the bases of the two flagellar bundles, which were always located on one hemisphere of the cell (Fig. 1 C). A flagellar bundle consisted of seven to nine separate flagella, each with a diameter of ~10 nm. Each flagellar bundle originated from an unusual electron-dense basal structure (Fig. 1 D). Whether each basal structure was a flattened disc could not be determined in negatively stained preparations of whole cells. Nor could it be determined whether each flagellum had its own motor, or whether each flagellar bundle had a single motor. Numerous pili were present on most cells, commonly observed in the area of the bases of the flagellar bundles (Fig. 1 C). Sulfur globules (Fig. 1 B) and polyphosphate deposits were common in the MC-1 cells grown with thiosulfate.

Cells of strain MC-1 collected in a sharp band at a specific low oxygen concentration within ~15 min after filling the capillary. Band formation resulted from aerophilic and aerophobic behavior, as is typical of microaerophilic bacteria (Fenchel, 1994; Zhulin et al., 1996). Respiration decreased the $[O_2]$ in the band, and the cells, seeking the preferred $[O_2]$, migrated toward the meniscus, i.e., opposite **B** (Fig. 2 A–C). Migration of the band stopped before it reached the meniscus (Fig. 2 D), presumably at a point where the rate of diffusion of oxygen to the band from the interface was equal to the rate of consumption of oxygen within the band. During migration, individual cells in the band swam parallel or antiparallel to **B**, reversing direction when they moved through the boundary of the band. If **B** was reversed during migration, cells swimming in either direction executed U-turns and continued swimming in the same directions relative to **B**, that is, away from the position of the band at the moment of field reversal. This tended to disperse the band. When **B** was subsequently restored to the original orientation, the band reformed and continued migrating opposite **B**. This result showed that cells could swim forward and backward relative to the field direction with their magnetic dipoles oriented parallel to **B** in both cases. In contrast, reversal of **B** caused *M. magnetotacticum* cells in an aerotactic band to rotate but not to swim away from
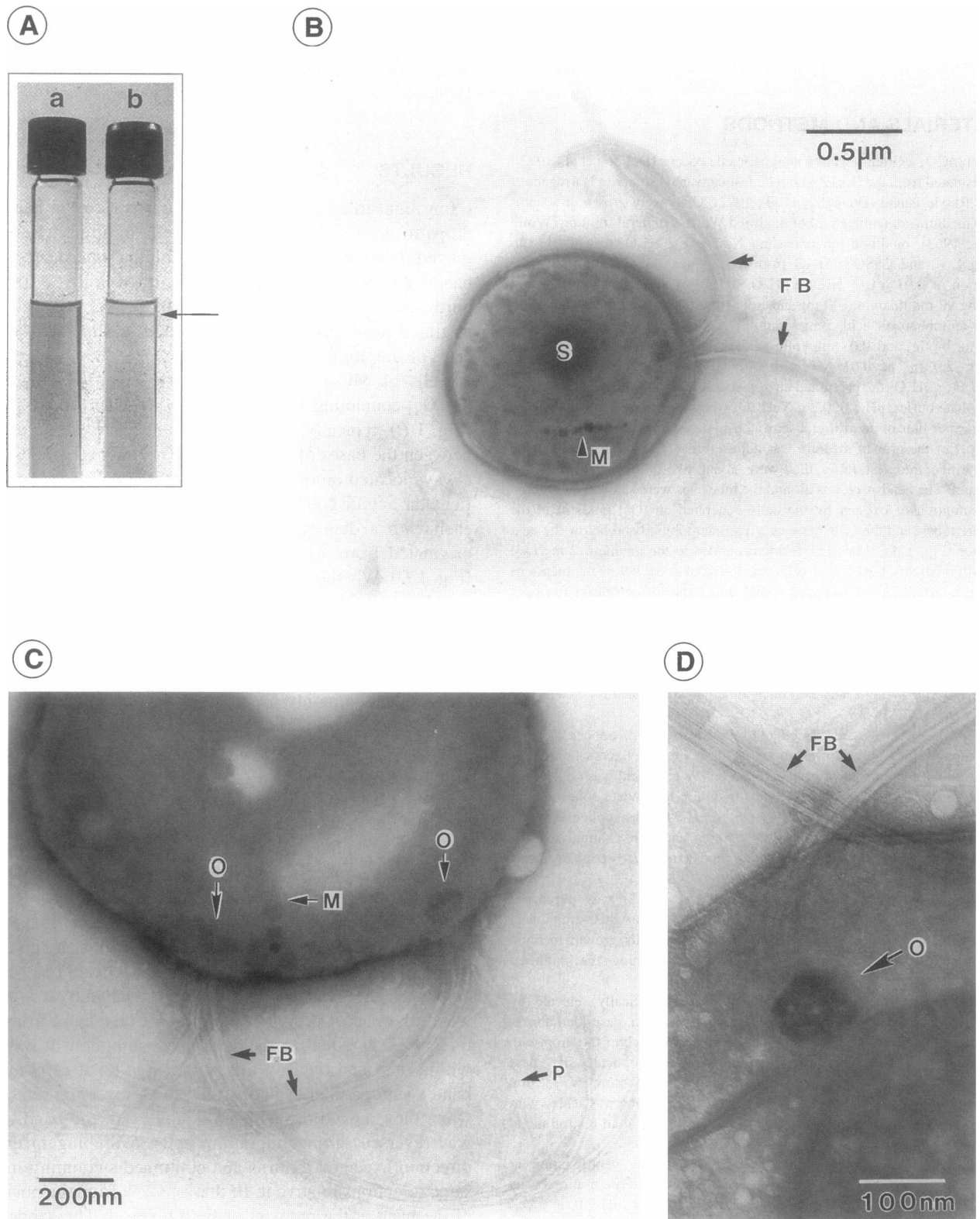
FIGURE 1   (A) Culture tubes with semisolid [O₂]-gradient medium containing thiosulfate and the redox indicator resazurin: (a) uninoculated medium; (b) medium inoculated with cells of strain MC-1. (B) Scanning transmission electron micrograph (STEM) of a negatively stained cell of strain MC-1, showing its coccoid morphology and bilophotrichous flagellation (two flagellar bundles; FB), chain of magnetosomes (M), and intracellular sulfur globule (S). (C) STEM of a portion of a cell of strain MC-1, showing the arrangement of flagellar bundles (FB) relative to the chain of magnetosomes (M), the two basal structures (O) from which the each of the two flagellar bundles originate, and the presence of numerous pili (P) that are likely responsible for the cells' ability to stick to each other and to surfaces. (D) High-magnification STEM of one of the basal structures (O) from which the flagellar bundles originate in the cell.
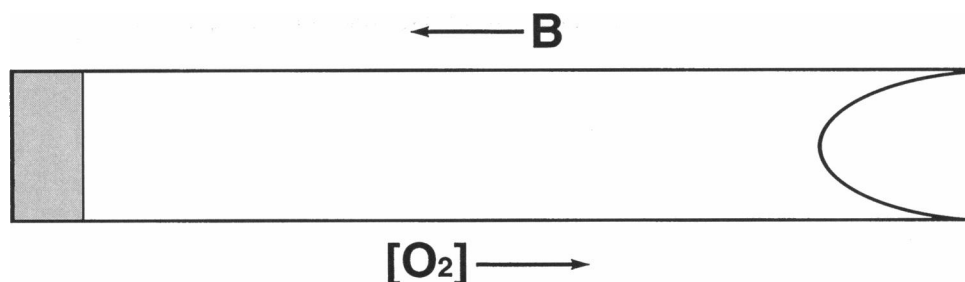
$$\longleftarrow B$$

$$[O_2] \longrightarrow$$

FIGURE 2 (*Top*) Schematic of flat capillary: (*left*) petroleum jelly plug; (*right*) open end and meniscus. Orientation of the magnetic field and direction of increasing $[O_2]$ are indicated by arrows. (*A–C*) Video frames, 1.5 min apart, showing migration of a band of cells of strain MC-1 to the right, opposite the magnetic field, toward the meniscus (higher $[O_2]$) in the capillary. The meniscus is out of the field of view. Arrows indicate stationary features that can be used to judge the motion of the band. (*D*) Stationary band near meniscus after migration. (*E*) Same view of capillary as in *D*, 30 min after perfusion with nitrogen gas. Most of the cells have moved up to the meniscus. (*F*) Same view of capillary as in *D*, 5 min after reperfusion with air. Most of the cells have reformed a band close to the original stationary position (*D*).
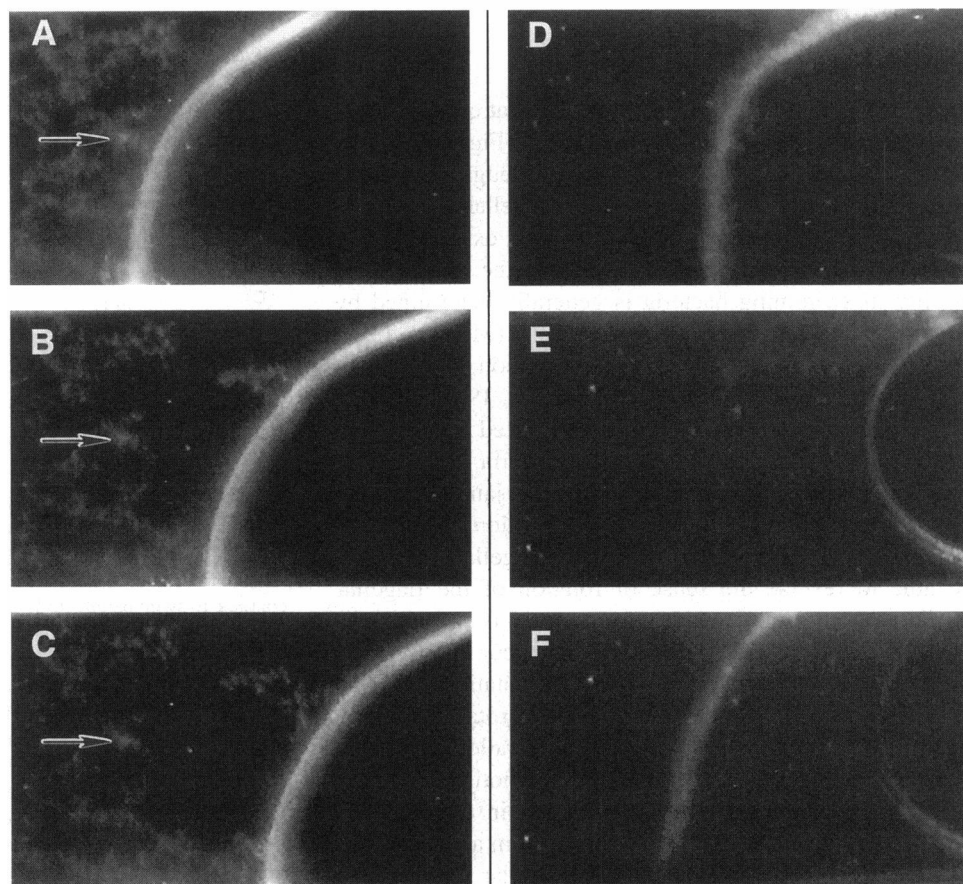
the band position. Thus the behavior of cells of *M. magnetotacticum* but not cells of strain MC-1 was invariant after reversal of **B**.

After the band of MC-1 cells had stopped migrating, most of the cells became immobilized on the walls of the capillary or attached to each other (Fig. 2 *D*), presumably because of the presence of numerous pili on the cell surface (Fig. 1 *C*). Some cells continued to make straight-line migrations, either parallel or antiparallel to **B**, through the band, while other cells executed short loops in and around the band. Increasing the magnetic field strength made the loops tighter, indicating that this type of motility involved rotation of the cells' magnetic dipoles away from **B**.

Perfusion of the capillary with pure nitrogen gas caused the band to migrate from its original position in air (Fig. 2

D) to the meniscus (Fig. 2 *E*). In this migration, the band did not move as a unit; rather, individual cells detached themselves from the band and swam antiparallel to **B** up to the meniscus. Upon subsequent reperfusion with air, the cells moved more rapidly away from the meniscus, and the band reformed close to the original band position (Fig. 2 *F*). This sequence of events was similar to the responses of bands of *M. magnetotacticum* bands and other microaerophilic bacteria (Fenchel, 1994; Zhulin et al., 1996) and is further evidence that the bacteria continually seek a preferred low concentration of oxygen.

When cells of strain MC-1 in the stationary band were illuminated with white, blue (λ_{min} = 330 nm), or yellow (λ_{min} = 500 nm) light, cells in straight line and looping motion began swimming parallel to **B**, away from the me-

niscus and toward the petroleum jelly plug. Eventually all of the cells, including the immobilized cells, left the band and accumulated at the petroleum jelly plug. Thus white, blue, or yellow light, but not red light, caused a response similar to an increase in [O_2]. When illumination was switched from white, blue, or yellow light back to red, cells subsequently reversed swimming direction to antiparallel to **B**, and swam back to the original position of the band. In contrast, there was no wavelength-dependent effect of illumination on bands of *M. magnetotacticum*.

DISCUSSION

These results demonstrate unequivocally that cells of strain MC-1 can swim in both directions along **B** (Fig. 2), and that the cells migrate to a preferred [O_2]. Although motility in coccoid bacteria with bilophotrichous flagellation, such as strain MC-1, has not been studied in detail, extensive studies in other cells have established that the direction of motility in swimming bacteria is generally determined by the sense of rotation of their helical flagella (Manson, 1992; Berg and Brown, 1972; Silverman and Simon, 1974; Alam and Oesterhelt, 1984; Zhulin and Armitage, 1993; Ordal et al., 1993). Whereas peritrichously flagellated bacteria and some lophotrichously flagellated bacteria can swim smoothly in only one direction because of jamming in the flagellar bundle when the sense of rotation is reversed (Macnab, 1977), other lophotrichously flagellated bacteria are able to reverse the sense of rotation of the flagellar bundle without jamming and swim smoothly in either direction (Alam and Oesterhelt, 1984). This could also occur in strain MC-1, with the sense of flagellar rotation regulated by an oxygen sensory system, as in other aerotactic bacteria (Taylor, 1983). As a result, cells swim parallel or antiparallel to **B**, depending on [O_2]. The looping motility observed in and around the immobilized cells was in tighter loops when **B** was increased, and could result from asynchronous rotation of the two flagellar bundles. Similar looping motility was observed in cells at the edge of the water drop in the standard assay.

The behavior of *M. magnetotacticum* bands is consistent with the temporal sensory mechanism (Segall et al., 1986), in which cells determine the change in [O_2] with time. For these cells, the role of **B** was axial, that is, **B** provided an axis, but not a direction, for motility along the [O_2] gradient, as shown by the fact that the aerotactic band did not disperse after a reversal in the direction of **B** (Fig. 3 *B*). Presumably, cells moving in either direction relative to **B** used the temporal sensory mechanism to sense that they were moving away from the preferred [O_2], reversed swimming direction, and returned to the preferred [O_2]. This kept the band intact.

However, the temporal sensory mechanism does not account for aerotaxis in strain MC-1, because it is inconsistent with the observation that reversal of **B** during migration resulted in cells swimming persistently either parallel or
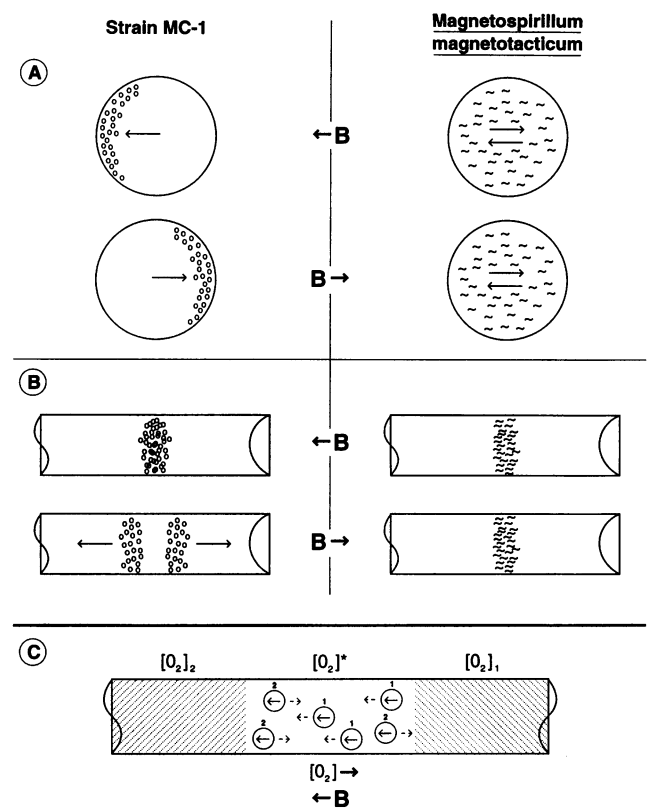

FIGURE 3 (*A*) Illustrations comparing the behavior of strain MC-1 and *M. magnetotacticum* in water drops on a microscope slide (standard assay). Cells of strain MC-1 swim persistently parallel to **B** (North-seeking motility) and accumulate at the edge of the drop. When **B** is reversed, cells continue to swim parallel to **B** and accumulate at the other side of the drop. Cells of *M. magnetotacticum* swim in either direction relative to **B**, and continue to do so when **B** is reversed. (*B*) Illustrations of aerotactic bands of strain MC-1 and *M. magnetotacticum* in flat capillaries. After reversal of **B**, MC-1 cells rotate 180°, and the band separates into two groups of cells, swimming in opposite directions along **B**, away from the position of the band before the reversal. A second reversal (not shown) results in the reformation of the band. For cells of *M. magnetotacticum*, reversal of **B** causes all of the cells to rotate 180°, but the band remains intact. (*C*) Illustration of the proposed two-state aerotactic sensory mechanism in cells of strain MC-1. [O_2] increases to the right. Cells have two sensory states, 1 and 2, that cause opposite directions of flagellar rotation, hence the swimming direction along **B**. State 1 causes cells to swim persistently parallel to **B** until they encounter a low oxygen threshold, [O_2]$_2$, which switches them into state 2. State 2 causes them to swim persistently antiparallel to **B** until they reach a high oxygen threshold, [O_2]$_1$, which switches them back to state 1. For swimming either parallel or antiparallel to **B**, the cellular magnetic dipole is oriented parallel to **B**. If **B** is reversed, cells in either state rotate 180°, causing them to swim away from the [O_2] threshold that would reset them into the other state. This results in dispersal of the band into cells moving in opposite directions, as illustrated in *B*. In the standard assay, diffusion of oxygen into the drop results in [O_2] > [O_2]$_1$, which switches all of the cells into state 1, causing them to swim persistently parallel to **B** (north-seeking motility).

antiparallel to the reversed **B**, away from the band (Fig. 3 *B*). If the MC-1 cells were using the temporal sensory mechanism for aerotaxis, they would have sensed they were moving away from the preferred [O_2], as the spirilla did, causing them to reverse direction and return to the band,

even after reversal of **B**. Thus, for strain MC-1, the role of **B** was polar, providing a direction as well as an axis for motility. Only one orientation of **B** with respect to the direction of the $[O_2]$ gradient allowed formation of an MC-1 aerotactic band.

The behavior of MC-1 cells fits a novel model for a two-state aerotactic sensory mechanism. In this model, the $[O_2]$ directly determines the sense of flagellar rotation and the swimming direction relative to **B** (Fig. 3 *C*). At an $[O_2]$ higher than the preferred $[O_2]$ (state 1), the flagellar motors rotate counterclockwise (ccw) and the cells swim parallel to **B**. At an $[O_2]$ lower than the preferred $[O_2]$ (state 2), the flagellar motors rotate clockwise (cw) and the cells swim antiparallel to **B**. The assignment of ccw rotation to swimming that is parallel to **B** is arbitrary, but is consistent with the ccw flagellar rotation for other species of bacteria swimming in the predominant motility direction. Cells persist in one of the two sensory states until they encounter the $[O_2]$ threshold that switches the sensory system to the other state, resulting in a reversal of swimming direction.

The two-state mechanism was consistent with the behavior of cells of strain MC-1 in the standard assay (Fig. 3 *A*), where diffusion of oxygen into the water drop resulted in an $[O_2]$ above the preferred $[O_2]$, which switched all of the cells into state 1, causing them to swim persistently parallel to **B** until they accumulated at the edge of the drop. Adaptation, i.e., spontaneous switching between the two states, apparently did not occur, as evidenced by the fact that no cells reversed swimming direction relative to **B** in a half-hour period, even though oxygen diffusion into the drop presumably resulted in a saturated, homogeneous medium.

Additional evidence for the two-state mechanism was seen in the behavior of individual cells that entered the aerotactic MC-1 band in the capillary tubes. The cells continued swimming in the same direction relative to **B** until they reached the opposite boundary of the band, with its lower (or higher) $[O_2]$ that switched the state of the cells. They then reversed direction and crossed the band to the boundary at which they entered, once more switching the state of the cell.

The two-state mechanism was also consistent with dispersal of the migrating band in the capillary tube after the reversal of **B** (Fig. 3 *B*), because after the field reversal, the cells in either state continued to swim parallel (state 1) or antiparallel (state 2) to **B**, but were now directed away from the $[O_2]$, lower or higher than the preferred $[O_2]$, respectively, that would have switched them to the other state and caused them to reverse direction relative to **B**.

The response of cells of strain MC-1 to white, blue, or yellow light was also consistent with the two-state mechanism, if we assume that the light overrode the actual $[O_2]$ and switched the cells to state 1, causing them to swim persistently parallel to **B**. When illumination ceased, the sensory system reverted to normal operation, and cells that had swum to an $[O_2]$ below the preferred $[O_2]$ were switched to state 2, reversing their swimming direction, and causing them to return to the band position.

Thus magnetotaxis in cocci, as in spirilla, is a form of aerotaxis, i.e., magnetically assisted aerotaxis, or magneto-aerotaxis, directing the cells to a preferred $[O_2]$. Because of the different role of the magnetic field and different aerotactic sensory mechanisms in the two cell types, the cocci and spirilla may be said to exhibit polar and axial magneto-aerotaxis, respectively. Thus the behaviors of Northern- and Southern-hemisphere spirilla with respect to migration along **B** in the standard assay are indistinguishable, whereas Northern- and Southern-hemisphere cocci swim persistently in opposite directions along **B** in the standard assay (Blakemore et al., 1980).

In either case, magneto-aerotaxis appears to be advantageous for bacteria in sites with vertical chemical stratification, and hence vertical concentration gradients. Because the oxygen gradient is aligned along the vertical component of the geomagnetic field, movement along the field would facilitate movement along the gradient. This reduces a three-dimensional search problem of locating and remaining at the preferred $[O_2]$, either in the water column, or, as in many freshwater sites, at or near the sediment-water interface (Spring et al., 1993), to one dimension and presumably increases the efficiency of the aerotactic response.

In chemically stratified, semianaerobic basins, perturbation of the oxygen gradient by such processes as wind-driven mixing might cause the bands to disperse, but the polar magnetoaerotactic response would cause the bands to reform as the gradient was reestablished, because cells that had migrated above or below the reforming OATZ would be switched into states 1 and 2, respectively, causing them to migrate along the magnetic field lines, back toward the OATZ.

Although there are a number of distinct species of magnetotactic cocci (Moench, 1988; Spring and Schleifer, 1995), they all apparently exhibit the phenomenon of polar magneto-aerotaxis, as described here for strain MC-1. Moench and Konetzka (1978) reported "magnetococci" in the water column of a sewage oxidation pond and in jar enrichments with high cell densities. If the high cell densities had resulted in depletion of oxygen in the sediments, polar magneto-aerotaxis would have caused the cells to migrate opposite the ambient magnetic field direction into the water column to find the preferred oxygen concentration.

Finally, the term "magnetotaxis" has been used to describe the orientation and migration of bacteria along geomagnetic field lines (Blakemore, 1975). However, the orientation of the bacteria in the magnetic field is a passive process due to the torque exerted on the permanent cellular magnetic dipole by the magnetic field (Frankel, 1984). Indeed, killed cells are also oriented in a magnetic field, but do not migrate. As reported here for cocci, and by Spormann and Wolfe (1984) for spirilla, migration in the magnetic field is determined by an aerotactic sensory system. Hence "magnetotaxis" in these organisms is actually polar or axial magneto-aerotaxis, respectively. This is probably true for all "magnetotactic" bacteria. However, there is also the possibility of magnetically assisted chemotaxis to

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molecules or ions other than oxygen, such as sulfide, or magnetically assisted redox taxis (Bespalov et al., 1996), in bacteria that inhabit the anaerobic zone in chemically stratified basins (Bazylinski et al., 1995) and sediments (Sakaguchi et al., 1993).

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